

Burrow structure and microhabitat characteristics of *Nesiergus insulanus* (Araneae: Theraphosidae) from Frégate Island, Seychelles

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Abstract. The burrow structure and microhabitat variables of the little known theraphosid *Nesiergus insulanus* Simon 1903 were determined on Frégate Island, Seychelles. The species constructed burrows in fossorial substrates, including rocks, leaf litter and bare soil as well as on the trunks of decaying trees, both recumbent and standing. The majority of burrows were predominantly found in sandy loam soil with partial protection from the sun. The density of burrows was determined to be weakly positively correlated to soil and substrate type and strongly negatively correlated to degree of exposure to the sun. The pH of the soil in which burrows are found was not significantly related to burrow sites, and variability in burrow structure was revealed. Burrow aggregations vary from single burrows to aggregations exceeding 100, distributed randomly.

Keywords: Tarantula, habitat, generalist

Little is known of the theraphosids of the Seychelles archipelago and published reports consist of little more than taxonomic descriptions and brief observations of their natural history (Simon 1903; Hirst 1911; Benoit 1978; Guadanucci & Gallon 2008; Saaristo 2010). More generally, despite numerous recently published papers on the behavior of tarantulas (Kotzman 1990; Fernandez-Montraveta & Ortega 1991; Costa & Pérez-Miles 1998, 2002; Quirici & Costa 2005), the biology and ecology of many tarantulas is poorly known (Carter 1997; Yáñez et al. 1999; Machkour M'Rabet et al. 2005).

Three species of *Nesiergus* are recognized and are likely endemic to Seychelles. *Nesiergus insulanus* Simon 1903 is the type species for the genus and is known from Frégate and L'Îlot Frégate Islands (Canning et al. 2013), with anecdotal and photographic evidence from naturalists on Cousine Island indicating that it may be more widely distributed than currently recognized. *Nesiergus halophilus* Benoit 1978 is known from Frégate, Récife, Silhouette and Curieuse; *Nesiergus gardineri* Hirst 1911 is known from Mahé, Felicite, Praslin, Silhouette and The Sisters (Guadanucci & Gallon 2008).

The burrows of these spiders, as with other members of the family, are used for protection against predators and parasites, for the protection of eggs and developing spiderlings, protection during ecdysis, for the capture of prey and for the control of thermal stress (Dippenaar-Schoeman 2002). Studies of habitat use by spiders have found that there are strong associations with abiotic factors such as structural features, temperature, wind, rain and humidity. Temperature and humidity have been shown to be critical factors influencing microhabitat selection for a number of spider species (Norgaard 1951; Williams 1962; Cherrett 1964; Sevacherian & Lowrie 1972; Riechert & Tracy 1975) and similar associations have been found with areas of high prey availability (Riechert & Gillespie 1986). Spiders are known to select high quality habitats (Morais-Filho & Romero 2008), and the structure of the burrows and the environmental parameters necessary for their construction must be known to

provide a better understanding of a poorly known species, its role in the community, and even as a potential indicator of habitat change.

METHODS

Study site.—Frégate Island (04° 35' 19"S, 55° 56' 55"E) is the most isolated of the Seychelles granitic islands (Ferguson & Pearce-Kelly 2004) and is situated 55 km east of Mahé Island (Skerrett et al. 2001). It is 219 ha in area, has an altitude of 125 m at its highest point and overlies oceanic basalt. Phosphatized granite and phosphate-cemented sandstone are associated with guano deposits on the plateau. The low-lying areas of the island were marshy in the past and are now characterized by sediments of fine clay and quartz (Braithwaite 1984). However, these marshy areas have been replaced, to the detriment of many species, by cultivated fields, gardens and a marina development.

Field methods.—Field sampling sites were determined by initially conducting a pilot study. The island was stratified into habitat types based on the vegetation map of Henriette & Rocamora (2009). Vegetation types were clearly distinguishable as a result of large-scale anthropogenically-induced vegetation changes. Ground truthing determined the precise location of these various habitats and in each described habitat an extensive search was conducted on three separate occasions. In each habitat type, we extensively searched leaf litter, overturned rocks and logs and searched all other litter to find burrows. This allowed us to determine the habitat types in which spider burrows occurred. These sites were exhaustively searched to ensure that burrows or signs of spiders were not missed. The habitat types that were found in the pilot study to support these spiders were the following (with number of sample sites per habitat type determined by random selection in parentheses): Coconut-dominated woodland (8), *Ficus benghalensis* (3), Mixed exotic woodland (7), Native woodland (6), Replanted native woodland (6), Hotel area native planted (4), Exotic scrub (8), Grassland (3) Coconut woodland planted with natives (3). Those habitats in which no burrows or other

signs of spiders were found included bamboo, coconut plantations with grassland, cultivated areas, orchards and *Scaevola*; these sites were not sampled further.

Subsequent to the pilot study, the island was stratified into numbered quadrats, each measuring 100 × 100 m. From these quadrats, a random integer generator (www.random.org) was used to obtain random sample quadrats in each vegetation type in which spiders were found in the pilot study, ensuring that approximately 25% of the island was represented. Sampling sites within these quadrats consisted of a 100 m × 2 m transect at right angles to the contour. Those vegetation types in which no burrows were found in the pilot study were excluded from the selection of sampling quadrats. Forty-eight quadrats were generated in this way and sampled, of which 38 sites contained burrow aggregations. We define an aggregation as a cluster of burrows within a distance of less than one meter from one another.

Burrow structure: Burrows were examined at the 38 sample sites. At each sample site, an individual spider was extracted from a burrow to confirm the identification of the species. This was completed after data from the particular burrow had been quantified. At each sample site in which burrow aggregations were found, we measured the diameter of the largest burrow and determined the orientation of all burrows. We noted whether each burrow's entrance was flush with the ground and whether debris was incorporated in the burrow entrance. The depth of the burrow could not be accurately determined without digging them up due to their varying shapes. To determine dimension and shape, five burrows were randomly selected, spiders were extracted and Plaster of Paris was poured down burrows to create an impression of the burrow. The volume of each of these burrows was determined by immersing the casts in a measuring cylinder of water and measuring the displacement. The dimensions and shape of burrows were also established by actively seeking burrows adjacent to rocks or other objects, such as coconuts or large fallen branches. At ten of these sites, objects were removed to expose a cross section of the burrow. These burrows were closely examined, measured and photographed to confirm shape, number of chambers, number of spiders within each burrow, use of silk and dimensions.

Microhabitat characteristics: Each sample site was visited in the early morning, at midday and late afternoon on at least three separate occasions only on sunny days for a three-month period to determine the temporal exposure of burrows to the sun. Burrows were considered to have full protection from the sun if they were in shade at each visit, partially protected if they were in sun on at least one visit and having no protection if they were exposed to the sun on each visit. We recorded a description of the habitat surrounding the burrow aggregation. The substrate was characterized as leaf litter, bare soil, woody vegetation, grass or other. Leaf litter (Fig. 1a) consisted of soil substrate covered with a complete layer of leaf litter with minimal or no soil exposed. The leaf litter varied from a single layer of leaves covering the soil to three to four layers of leaves. Bare soil (Fig. 1b) consisted of a substrate of exposed soil, with leaves sporadically scattered over the substrate, but not to the extent that they entirely covered the substrate. Woody vegetation represented burrow sites where the burrow had been constructed in living plant

material such as roots. Grass (Fig. 1c) consisted of the substrate being covered in a layer of living grass. Other represented burrows were constructed in rocks (Fig. 1d), coral remnants or decaying tree trunks (Figs. 1e, f).

Ambient and burrow temperature and humidity were recorded using a thermistor digital instrument with penetration probe. Soil characteristics were determined by collecting three soil samples of approximately 500 grams each from each site and the basic soil texture, pH, soil type and soil moisture were determined. Soil texture was determined by using the United States Department of Agriculture soil triangle (online at http://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/edu/?cid=nrcs142p2_054311). Soil moisture was determined by using the soil moisture content standard test method of the Australian Department of Sustainable Natural Resources. Each soil sample was weighed, dried in an oven at a constant temperature of 110 °C for 4 hours and then weighed again after cooling. The moisture content was determined as weights compared before and after drying expressed as a percentage. Soil sampling was conducted in the dry season to discount the influence of rain on moisture content. The pH of the soil samples was determined with the use of a Bluelab combometer calibrated to pH 7.0 before the testing of each soil sample.

Spiders were also observed under captive conditions. Twenty females, including four mature specimens, were kept in a confined situation in a communal polystyrene box (63 × 29.5 × 17 cm) and with a layer of soil 8 cm deep. The top of the box was covered with a glass sheet to prevent escape and for observation purposes. Spiders were provided with fresh water daily and food once a week. Burrowing behavior was observed under these conditions.

Analyses: One-way ANOVA was used to compare the number of burrows found in the sample sites with the microhabitat characteristics to determine whether there were any statistically significant differences. The analyses included those sample sites in which no burrows were found in the habitat types that were found to include burrows in the pilot study. Correlations were used to determine relationships between burrow densities and various microhabitat variables. Nearest neighbor analysis was adapted for this study to determine the patterning of burrows within an aggregation. As the method eliminates the effect of scale, the patterning within the distribution of the burrows in a cluster was determined (Rossbacher 1986). The formula used to determine aggregation distribution was $Rn = 2\bar{d}\sqrt{n/a}$ where the value of Rn represents the degree to which an observation departs from a predicted random distribution and \bar{d} = the mean distance between the nearest neighbors, n = total number of points and a = area under study. Rn ranges between 0 for a clustered distribution, 1.00 for a random distribution and 2.15 for a regular distribution (Clark & Evans 1954). Nearest neighbor analysis was used only at sites where there were more than 30 burrows in the aggregation ($n = 15$ sites). A Rayleigh test was used to determine whether the direction of the burrows was random or non-random.

RESULTS

Microhabitat characteristics.—The number of burrows in each sample site varied between habitats from no burrows to 134 burrows in aggregations. The mean aggregations and



Figure 1a–f.—Substrate types in which burrows of *Nesiergus insulanus* are found on Frégate Island, Seychelles. a. Leaf litter; b. Bare soil; c. Grass; d. Rock; e. Tree trunk with arrows indicating position of burrows approximately 1.5 and 1.7 m above ground level; f. Recumbent rotting log.

densities per square meter combined from sample sites in each habitat type were as follows: Exotic scrub 8.4 at 0.042/m², native woodland 36 at 0.18/m², coconut-dominated woodland 11.4 at 0.057/m², *Ficus benghalensis* 36.5 at 0.1825/m², mixed exotic woodland 6.5 at 0.01/m², grassland 3.5 at 0.0175/m², hotel area native planted 15.4 at 0.0775/m², coconut woodland planted with natives 1.7 at 0.0085/m² and replanted native woodland 21 at 0.105/m². Microhabitat variables varied between sample sites (Table 1) with the mean ambient temperature found to be 2.13°C higher than the temperature within the burrows across habitat types. In contrast, the humidity within the burrows was found to be an average of 9.93% higher than the ambient humidity. Open grassland was the only habitat in which at least some burrows were found to be fully exposed to the sun. The mean ambient temperature for grassland was 2.5° C warmer than the mean across all habitat types. The mean seasonal change in temperature is in a very narrow band and this is reflected in the mean temperature across habitat types.

An ANOVA showed a significant difference in number of burrows between substrates across sample sites ($F_{3, 32} = 3.42$,

$P = 0.03$) with leaf litter and bare soil being preferred over other substrates. A follow-up test to determine differences between these two substrates showed that there is no significant difference in choice between bare soil and leaf litter ($F_{1, 16} = 0.09$, $P = 0.77$) as the more frequently used substrates. Few burrows were found in grass-covered areas and in the cracks and holes of rocks. Those burrows dug in bare soil were found among vegetation and often close to rotting logs that provided protection and a supply of prey in the form of termites or other invertebrates. There was a significant difference in soil types in which burrows occurred ($F_{7, 64} = 5.66$, $P < 0.0001$) with the majority being found in sandy loam. Protection from full exposure to the sun was statistically highly significant ($F_{2, 24} = 11.13$, $P = 0.0003$) with spiders preferring partial protection from the sun. There was a non-significant correlation between the soil types and the density of burrows (Spearman Rank correlation, $r = 0.167$, $P = 0.157$), a significant correlation between choice of substrate and burrow density ($r = 0.357$, $P = 0.013$) and a very strong correlation between protection from the sun and burrow densities ($r = 0.9995$, $P = 0.001$). The soil pH varied

Table 1.—Summary of microhabitat variables across habitat types for burrows of *Nesiergus insulanus* on Frégate Island. Figures given are the percentages of the total number of burrows displaying that particular variable for the habitat type. Moisture content, pH and temperature measurements are from the lowest to the highest recorded measurement at each site in the specific habitat. FB = *Ficus benghalensis*, CWPWN = coconut woodland planted with natives, MEW = mixed exotic woodland, ES = exotic scrub, NW = native woodland, RNW = replanted native woodland, HANP = hotel area nativeplanted, CDW = coconut dominated woodland, GL = grassland.

	FB	CWPWN	MEW	ES	NW	RNW	HANP	CDW	GL
Sampling sites (N)	3	3	7	8	6	6	4	8	3
Wind Protection									
none	66								50
partial	33	33		57.1	25	80	50	37.5	50
full		66	100	42.8	75	20	50	62.5	
Sun Exposure									
none		33	75	14.2	25			50	
partial	100	66	25	85.7	75	100	100	50	50
full									50
Substrate									
bare soil	33	33	50	71.4		60	50	37.5	
leaf litter	66	33	50	14.2	100		50	37.5	
grass									100
other(vegetation)		33		14.2		40		25	
Soil Characteristics									
silt loam				28.5					50
loam			25				100	12.5	
loamy sand		33	25	14.2		40		25	
silt	33								
sandy loam	33	66	50	42.8		20		62.5	50
sandy	33								
other (rock)						20			
moisture Content	10–71%	5–6%	6–23%	3–23%	12–27%	1–25%	10–15%	4–25%	6–10%
pH	4.2–4.9	6.1–8.9	5.7–8.2	3.7–7.4	4.9–8.5	5.1–8.3	5.2–8.4	5.7–8.9	7.3–8.2
Ambient Temp. (°C)	30.8–32.9	30.4–30.5	27.1–30.4	30.1–34.1	29.9°–31.8°	29.5°–31.5°	31.6°–32.1°	29.8°–31.5°	32.9°–33.5°
Burrow Temp. (°C)	28.0–31.2	27.9–29.1	25.7–27.3	27.6–32.3	27.1°–28.7°	27°–30.8°	28.4°–30.4°	26°–29.7°	31.8°–32.2°

considerably between habitat types and between sample sites, from 3.7 to 8.9 with a mean of 6.45 (UCL = 6.92, LCL = 5.98). A linear regression analysis determined that the relationship between pH and spider densities was non-significant ($r = 0.9815$, $P = 0.33$) and therefore plays no role in burrow site selection.

Burrow structure.—Nearest-neighbor analysis showed that the distribution of burrows within an aggregation was random, (average $R_n = 1.17$). These spiders make use of both fossorial substrates (Figs. 1a–c) and the trunks of decaying trees. The trunks of rotting trees, both standing (Fig. 1e) and recumbent (Fig. 1f) were used. The decomposing wood likely provides a regular supply of food to prey on such as termites and other invertebrates as well as providing a stable microclimate. Hollows and cracks in rocks were exploited on occasion (Fig. 1d). Spiders were also found under rocks where either a silk-lined depression or a burrow was constructed.

Captive specimens of *N. insulanus* were able to excavate their own retreats and were able to burrow through wood and roots, despite lacking a rastellum. When disturbed or if their burrow was damaged or destroyed, they excaevated a new burrow. Chelicerae were used in loosening the soil and the first pair of legs was used to pass the soil to the side of the burrow entrance or under the body where the third and fourth pairs of

legs pushed the soil from the burrow. The first one-third to one-quarter of the inside of the burrow was lined with silk. There were no silk mats or trip lines around the burrow entrance for prey detection. Silk was used in bends in burrows to support the walls at these bends (Fig. 2).

The majority of the burrow entrances lay flush with the surface and had no debris, although some debris in the form of small stones, sticks and millipede droppings were on occasion attached to the silk around the lip of the burrow. Burrows in the cracks of rocks were fully constructed of silk with debris, including feathers, attached along the full length of the burrow. A single entrance was observed at all burrows. These entrances were closed with silk with soil attached when the spider was in the process of ecdysis, incubating, when there were pre-emergent spiderlings in the maternal burrow, or under adverse weather conditions, such as during heavy rain. The entrances were completely camouflaged with soil during this period.

The largest burrow diameter found at sample sites was 13.59 mm with a mean diameter for all sampled burrows of 6.42 mm. Orientation of the burrow entrance of 116 burrows in all habitat types was determined and a Rayleigh test indicated that there was no particular prevailing orientation of burrow entrances ($Z = 0.282$, $P = 0.50$). Burrow shape was widely diverse and a single distinguishing shape cannot be

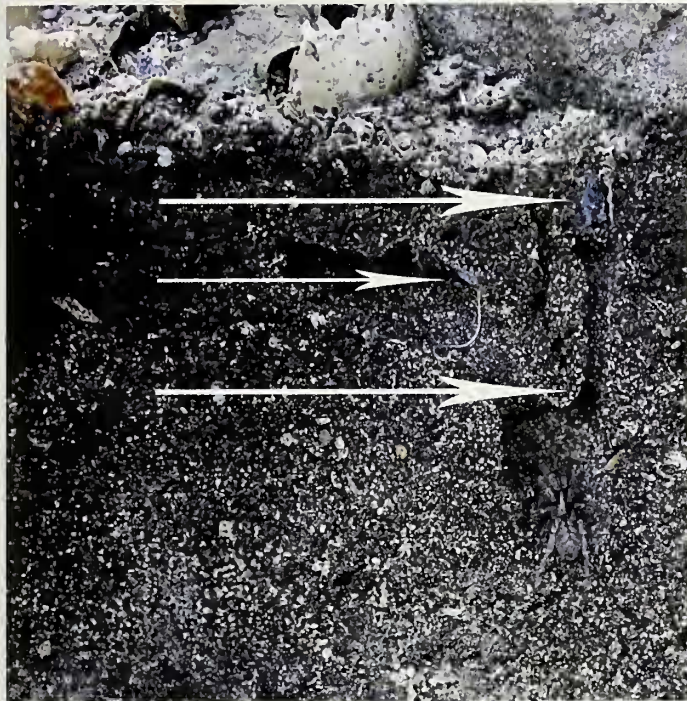


Figure 2.—Burrow of *N. insulanus* with resident spider in first chamber. Arrows indicate use of silk below burrow entrance, at curve above first chamber and on roof of second chamber.

attributed to this species. Burrows were J-shaped, U-shaped and V-shaped with variations of these basic profiles. Variations included additional chambers or shafts. Variations were sometimes due to an obstruction that the spider could not burrow through or around and sometimes appeared to be random. U-shaped variations included burrows recumbent with an extended burrow entrance. V-shaped burrow variations included additional horizontal arms or supplementary arms giving the burrows a Y-shape, and the dimensions of observed burrows varied widely (Fig. 3). The displacement volume of the five burrow molds were 22 ml, 41 ml, 53 ml, 10 ml and 7 ml.

DISCUSSION

Nesiergus insulanus makes use of a number of available substrate types including soil, tree trunks and cracks in rocks in which to create burrows. The exploitation of these substrates indicates adaptability that allows the species to exploit a wider range of habitats than would be available to more specialized species. This behavior could be considered an obligatory adaptation to their occurrence on small and isolated islands with limited resources, thus restricting their ability to occupy a more specialized niche.

Machkour M'Rabet et al. (2007) found that densities of the tarantula *Brachypelma vagans* Ausserer 1875 were dependent on soil type. This study also found significant associations with soil types, the type of soil apparently being important in burrow construction because of the possibility of collapse when these spiders only partially line their burrows with silk. The variation in burrow structure from simple, single-chambered structures to fairly complex constructions that are found in high densities in suitable habitat has also been recorded in *B. vagans* (Machkour M'Rabet et al. 2007).

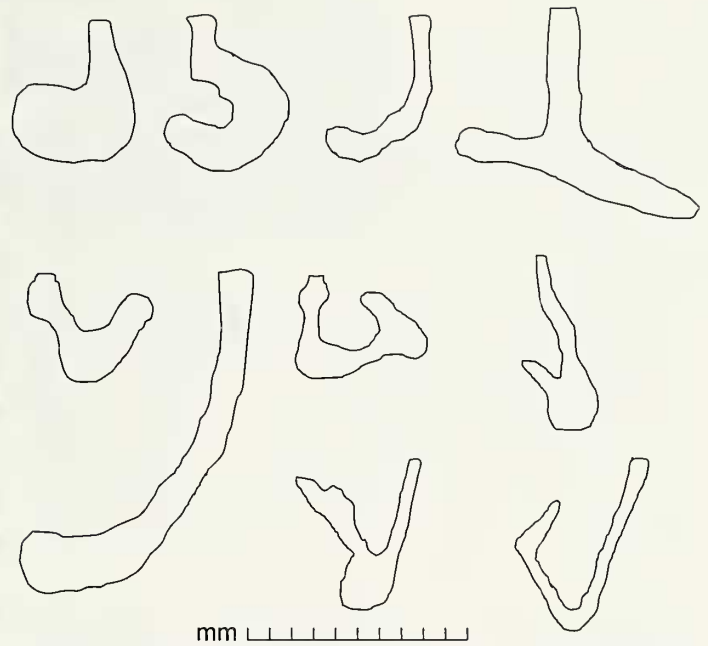


Figure 3.—Burrow shapes of *N. insulanus* indicating diverse shapes, including basic burrow shapes, as well as variations thereof, with additional chambers and shafts.

The combination of a number of suitable microhabitat variables appears to be necessary to support a population of these spiders and where these variables are absent, so too were the spiders. They were commonly found adjacent to rocks and decaying logs, as well as on pathways. These logs and rocks as well as roads and pathways provide ecotones that support increased biodiversity and productivity (Risser 1995). Arthropods have been found to be greatly influenced by changes in temperature and humidity (Cady 1984) and we found that sites of burrows that were at least partially protected from sun exposure, thus limiting fluctuations, were preferred over sites that offered little protection from the elements. Burrows found in exposed areas were few in number and even these were offered a degree of protection close to the ground.

The disturbance and alteration of natural habitats and the introduction of alien plant species is detrimental to the distribution of the species. Large-scale changes to the native vegetation on the island limits the opportunity for dispersal to new habitats and is cause for concern for a species with a limited distribution. Frigate Island has been severely degraded and large areas of the island are covered in alien species. In particular, monospecific stands of coconuts, *Cocos nucifera*, cover vast areas of the island, severely reducing available native habitat. The occurrence of these spiders in such degraded habitats is limited or absent and is of concern for the long term welfare of the species. As tarantulas do not balloon as a means of dispersal (Jankowski-Bell & Horner 1999) and spiderlings do not wander greatly if a suitable patch is found in which the spiderlings are able to burrow (Cutler & Guarisco 1995) their dispersal capabilities are reduced. The restoration of habitat and the creation of corridors between restored habitat and habitats in which this species is to be found are essential for the long term viability of the species.

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